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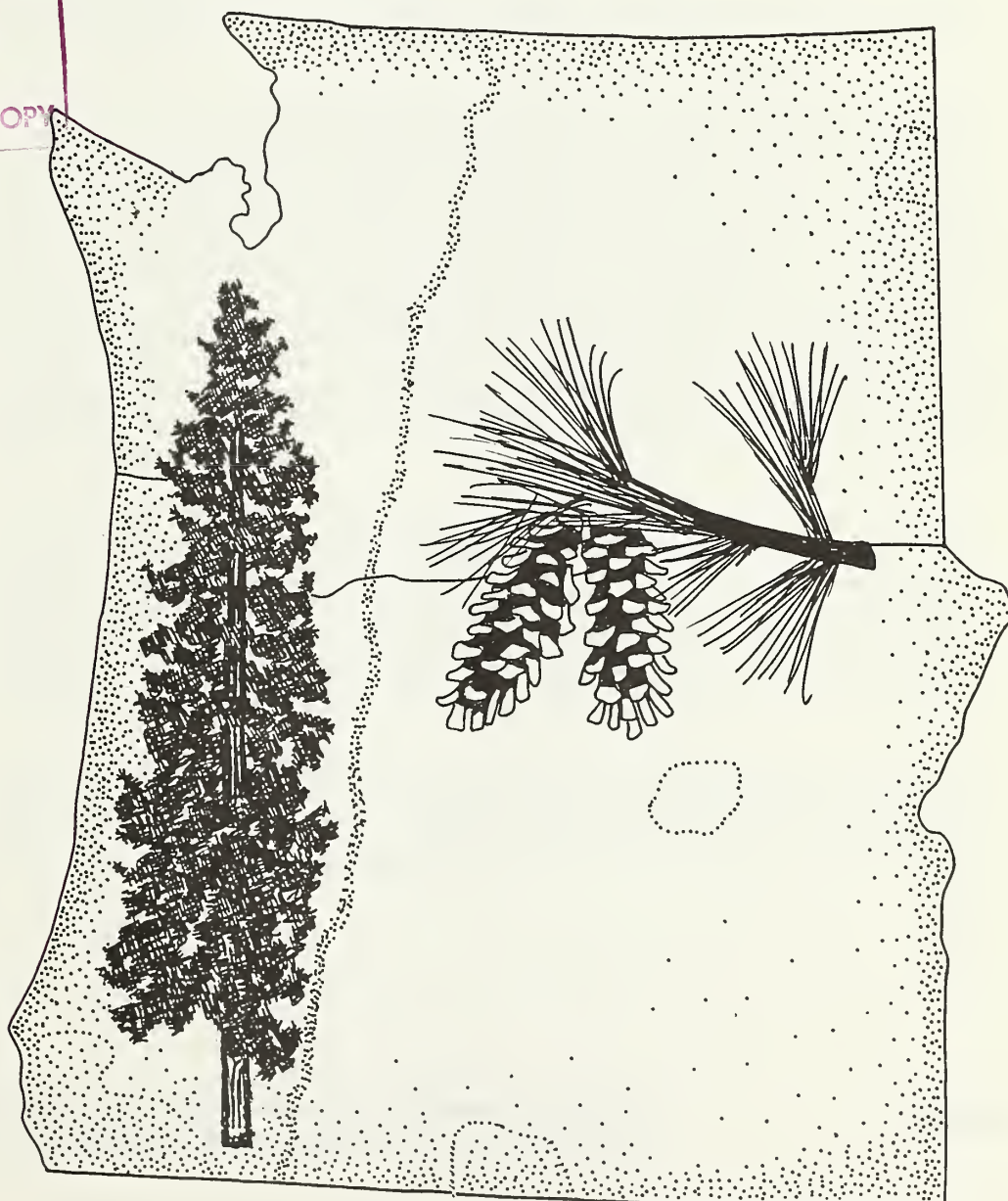
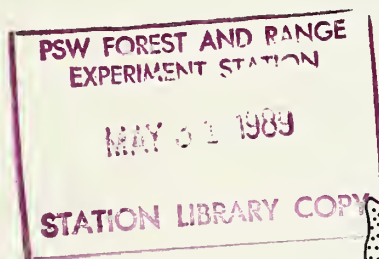
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Seed Zones and Breeding Zones for White Pine in the Cascade Range of Washington and Oregon

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Abstract

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Provisional seed zones and breeding zones were developed for white pine (*Pinus monticola* Dougl. ex D. Don) in the Cascade Range of western Washington and Oregon. Recommendations were based on genetic variation patterns obtained by evaluating genotypes of trees from 115 locations. Genotypes controlling growth vigor and growth rhythm were assessed in common gardens. Five zones, delimited mainly by latitude, were recommended: two in Washington, two in Oregon, and one in both States adjoining the Columbia River.

Keywords: Genetic variation, geographic variation, adaptation (plant), seed-transfer, *Pinus monticola*.

Summary

This paper reports new seed-transfer zones based on genetic variation patterns for white pine in the Cascade Range. Seedling progeny of 174 trees from 143 locations in western Washington and Oregon were grown as families in common gardens to evaluate the genotypes of parents. Two principal components of genetic expression (growth vigor and growth rhythm) described the adaptive differences among families. For Cascade provenances, most of the variation among families in the principal components was contributed by families within local populations. Most of the variation among populations was associated with latitude and distance east and west of the Cascades crest and little with elevation. Four non-Cascades provenances (from eastern Washington and Oregon and southern Oregon) were tested for their affinity with Cascades provenances. Only the two in southern Oregon were different, but the test lacked power.

The structure of genetic variation in the Cascades—most variation within locations and little between locations—is similar to that found in white pine elsewhere. Three hypotheses can be invoked to explain this structure: (1) the species is somatically plastic, or (2) the habitat nooks in which the species is found are environmentally homogeneous even though sometimes separated by hundreds of kilometers, or (3) the species emphasizes genomic flexibility at the expense of genomic stability. The study supplied no clear evidence to choose among hypotheses.

Because of the genetic structure of the species, the five suggested seed zones are quite large. Seed lots transferred within a zone may not be adapted, however, to all potential planting sites within the zone. Strictly speaking, zones have meaning only for sites presently occupied by white pine.

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Introduction

Breeding zones presently being used for white pine (*Pinus monticola* Dougl. ex D. Don) in Washington and Oregon are modified from a seed zone map established by the Western Forest Tree Seed Council (Oregon, Washington [Tree Seed Zones] 1966). Zones therefore do not reflect the genetic structure of the species because such information was not available in 1966. This paper reports provisional seed and breeding zones for the Cascade Range in Washington and Oregon based on procedures previously used for other species in western Oregon (Campbell 1986, Campbell and Sugano 1987).

White pine's niche is unusual among western conifers. The species is relatively intolerant of shade and moisture stress, and as a seedling, of cold, unless under deep snow or otherwise protected from frost heaving or winter wind. Because it grows very slowly for the first 10 to 15 years (Bingham and others 1971), it is competitively handicapped compared with many other seral species. Despite this restrictive niche, white pine occurs as a minor component in many of the forest zones of western Washington and Oregon and as a major component in the *Tsuga heterophylla* zone in Idaho (Franklin and Dyrness 1973). In the coastal region of the Pacific Northwest, it is commonly found in areas with special features causing unusually poor growth in the dominant species: in northern Washington, on glacial drift and outwash, forested swampland, and ultramafic soils (Franklin and Dyrness 1973); and in Oregon, on lava flows and serpentine (Whittaker 1960).

In western Washington and Oregon, white pine is most prominent as a minor seral species in those forest zones (*Abies amabilis*, *Abies lasiocarpa*, and *Tsuga mertensiana*) contributing extensively to the forested area of high elevations in the Cascades Range. It occurs as a major seral species (in small localized areas) only in the *Abies grandis* and *Tsuga heterophylla* zones on the eastern slope of the Cascade Range in Washington and in the *Abies magnifica shastensis* zone of southern Oregon (Franklin and Dyrness 1973). It is not a climax species in any forest zone in the Pacific Northwest or northern Idaho (Daubenmire 1966).

Rapid height-growth (up to 1 m per year on good sites) of white pine begins after about age 15 and may continue for more than 100 years (Bingham and others 1971). Trees of good size with high-quality wood are found even at high elevations, which makes the species a good candidate for artificial regeneration in some areas in the Cascade Range. Seed-transfer guidelines for white pine would therefore be helpful for reforestation in the Cascades.

Materials and Methods

The study primarily sampled the range of white pine in the Cascade Range of Oregon and Washington. In the Cascades, seeds were collected from 146 trees as part of the blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.) breeding program centered at Dorena, Oregon (figs. 1 and 2). Most trees were geographically separated, but in 31 cases two trees, differing in location by less than 1.6 km and in elevation by an average of 37 m, were sufficiently close to one another to be considered as two samples from a single location. An additional 28 trees originated elsewhere: 4 from northeastern Washington, 3 from the Strawberry Mountains in northeastern Oregon, 7 from the Lakeview area east of the Cascades in southern Oregon, and 14 from the Siskiyou Mountains west of the Cascades in southern Oregon. Site variables measured at each location were latitude in degrees, distance east and west of the crest of the Cascades in kilometers, and elevation in meters.

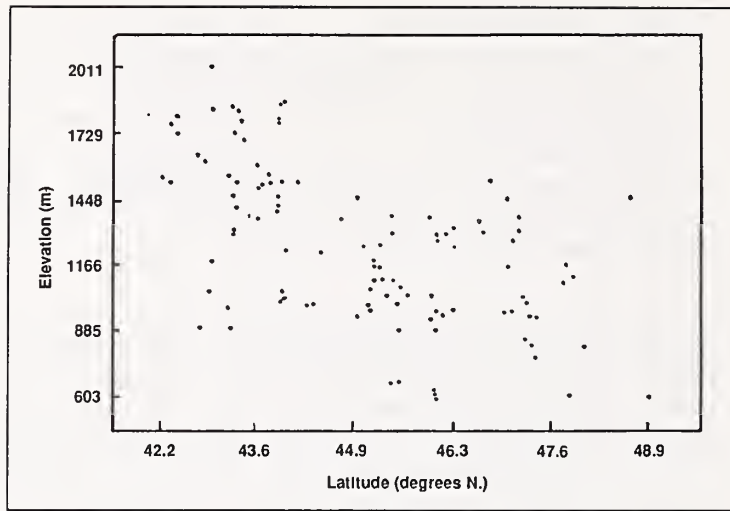


Figure 1—Distribution of parent-tree locations by latitude and elevation in the Cascade Range.

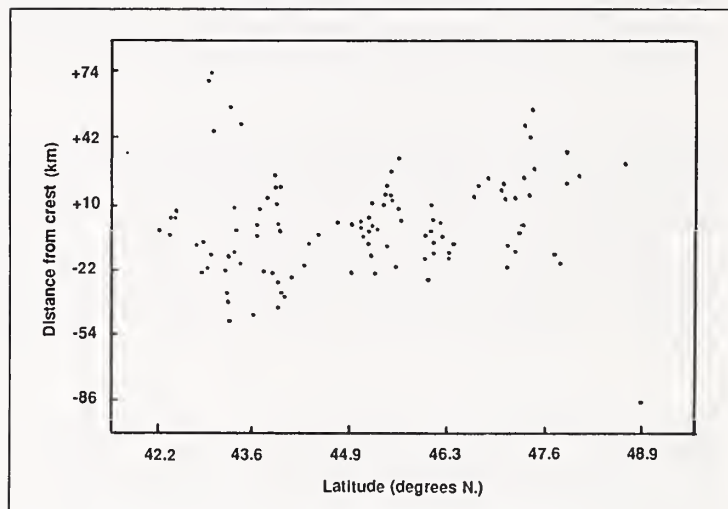


Figure 2—Distribution of parent-tree locations by latitude and distance west (–) and east (+) of the crest of the Cascade Range.

Genotypic values of parent trees were estimated by growing progeny (families) of wind-pollinated trees in seed incubators and in two common-garden environments in a nursery at Corvallis, Oregon. The two common gardens were planted in different years. In the first environment, germinated seeds of the 174 parent trees were planted in randomly assigned locations of five-seedling family row-plots in each of four replications. In this environment, a warm treatment was imposed by burying heating cables 15 cm below the soil surface and by covering the bed with a polyethylene tent. These treatments were applied only in spring and autumn to extend the growing season. Although temperature was not measured, previous experience suggests that it probably exceeded the ambient by 0 to 10 °C, depending on cloud cover and time of day or year. The second environment, planted to an identical design 1 year after the first, had no imposed treatment.

Table 1—Trait code, dates, and units of measurement of seedling traits in warm (W) and cool (C) nursery environments

Code ^a	Date measured	Measurement units
WCO	June 6, 1982	Number
WHT11	Dec. 15, 1982	Centimeter
WBB2	Mar. 11-Apr. 28, 1983	1/2-week classes
WHT21	Mar. 16, 1983	1/2-cm classes
WHT22	Mar. 23, 1983	1/2-cm classes
WHT23	Apr. 5, 1983	1/2-cm classes
WHT31 to WHT38	8 dates at about 2-week intervals from May 8-Aug. 10, 1984	1/2-cm classes
WHT41	Apr. 17, 1985	1/2-cm classes
WHT42	Oct. 7, 1985	1/2-cm classes
WDI	Oct. 7, 1985	Millimeter
CCO	June 1, 1983	Number
CHT21	Mar. 1, 1984	1/2-cm classes
CBB3	Apr. 4-May 2, 1985	1/2-week classes
CHT31 to CHT36	6 dates at about 2-week intervals from June 11-Aug. 17, 1985	1/2-cm classes
CDI3	Oct. 14, 1985	Millimeter
SDWT	Mar. 1-17, 1982	50 seeds (g)
DRMN	Apr. 15-May 16, 1983	(Days to germination-1)
DRSD	Apr. 15-May 16, 1983	(Days to germination-1)

^a The first character in the code designates the nursery environment, the next 2 characters the trait, the first numeral the growing season, the second the place in any sequence of measurement; for example, WHT22 is the warm-bed total height, second season, second measurement. Traits are total height (HT), bud flush (BB), total diameter (DI), mean germination rate of 50 seeds (DRMN), standard deviation of rate of germination (DRSD), seed weight of 200 seeds (SDWT), and cotyledon number (CO).

To evaluate adaptive genotypes adequately, some of the traits measured must be indexes of growth rhythm because shoot extension and cambial growth must be fitted within the frost-free period. Determining the cessation of height extension is especially difficult in pines; therefore, several measurements of total height were made yearly, especially in the third growing season. Serial measurements should reveal variation in the initiation, rate, duration, and cessation of elongation (Rehfeldt and Wykoff 1981). Furthermore, differences among genotypes in growth rhythm should be reflected in the matrix of genetic correlations among height measurements taken during the growing season. In the third season, only two seedlings were measured per plot, the same two throughout the schedule. Other traits measured were stem diameter, seed weight, germination date, and cotyledon number (table 1).

Data were analyzed and seed-zones delimited by procedures used previously in similar experiments with other species (Campbell 1986). The analysis involved 11 steps: (1) analyzing variance (or covariance) of data from each environment for each trait (or combination of two traits) according to the classification design (table 2); (2) estimating components of variance and covariance, additive genetic variance, and heritability at the individual seedling level; (3) estimating genetic correlations between

Table 2—The partition of variation among seedlings of 174 families from sources of variation, and the expected mean squares used in estimating components of variation

Sources of variation	Degrees of freedom	Expected mean squares ^a
Replications	3	
Locations	142	$\sigma_w^2/k + \sigma_p^2 + 4\sigma_{f(s)}^2 + 4.8632\sigma_s^2$
Families in locations	31	$\sigma_w^2/k + \sigma_p^2 + 4\sigma_{f(s)}^2$
Plot error	519	$\sigma_w^2/k + \sigma_p^2$

Within plot	^b	σ_w^2/k

^a σ_w^2 = effects of individuals within plots, σ_p^2 = plot effects, $\sigma_{f(s)}^2$ = effects of families within locations, σ_s^2 = effects of locations; k = harmonic mean of number of individuals within plot—4.1 and 3.0 for initial and final yearly measurements in the warm nursery bed and 4.9 and 4.8 for initial and final measurements in the cool bed, but k = 2 for all growth measurements taken within the growing season.

^b Number of degrees of freedom = about 2400 for initial and final yearly measurements and 690 for within-season growth measurements.

traits at both the location and family levels of genetic variability; (4) reducing the dimensions in the data by a principal component analysis of a genetic correlation matrix; (5) calculating factor scores from the eigenvectors for each significant principal component; (6) describing the pattern of genetic variation in factor scores for each principal component by a regression analysis (backward stepwise, Draper and Smith 1966) using indexes of parent tree habitat as predictive variables; (7) calculating lack of fit by using variation among trees at a location as pure error (Draper and Smith 1966); (8) mapping genetic variation patterns by using predictions from regression equations in step 6 above; (9) dividing the region into tentative seed zones based on the visual inspection of genetic variation patterns; (10) calculating an index of risk as the fraction of nonoverlap between the distributions of factor-scores within the native and introduced seed source (Campbell 1986, 1987); and (11) repeating step 10 two hundred times in each tentative zone, each time representing one hypothetical transfer between a randomly chosen plantation site and a randomly chosen seed origin (Campbell and Sugano 1987). Steps 9, 10, and 11 were repeated until fewer than 5 percent of transfers within a zone created risks greater than 0.5. The average risk associated with such zones should be less than 0.25; that is, within such zones, about 25 percent of planted seedlings are expected to be poorly adapted in comparison to indigenous seedlings (Campbell 1987).

Results

The classification model partitioned variation among seedlings into effects of parent-tree location (σ_s^2), trees(families)-within location ($\sigma_{f(s)}^2$), variation among plots (σ_p^2), and variation within plots (σ_w^2). The variation among open-pollinated families was taken to estimate one-third of the additive genetic variation within populations because white pine usually grows in isolated small stands or as isolated individuals. Pollination probably includes crossing among relatives or selfing. Genetic correlations among family members is therefore probably nearer to 0.33 than to 0.25. The within-plot variation included genetic variation within open-pollinated families (two-thirds of

Table 3—Analysis of variance for traits (for all 143 locations, 31 families within locations) and for factor scores of principal components

Trait ^a	Mean	Total variance ^b	Percentages of total variance			
			Among locations	Among families	Among plots	Within plots
			σ_s^2	σ_f^2	σ_p^2	σ_w^2
WHT11	3.23	0.0665	10.9+	12.2**	25.4**	51.5
WHT31	19.66	41.7195	18.5*	13.0**	13.9**	54.5
WHT38	22.57	47.9739	20.1**	10.7**	14.2**	55.0
WHT41	24.13	58.2718	19.7**	11.0**	14.5**	54.8
WHT42	34.12	135.3838	16.1*	11.8**	15.7**	56.4
CHT21	3.97	0.7181	19.0**	8.4**	19.6**	53.0
CHT35	7.26	2.9368	12.1+	11.7**	10.6**	65.7
CHT36	17.27	32.9458	13.1*	12.7**	16.0**	58.1
WDI4	7.39	5.1683	9.9	13.4**	25.9**	50.8
CDI3	5.59	1.5153	6.2	14.5**	4.9**	74.4
SDWT	9.69	5.2841	45.1*	51.6**	3.4	
GNMN	18.28	54.7862	3.4	80.1**	16.4	
GMSD	7.49	16.3337	28.0+	46.5**	25.5	
PC-1	6.00	2.1324 ^c	60.5**	39.5		
PC-1	6.17	1.7795 ^d	48.8**	51.2		
PC-2	14.51	3.2712 ^c	40.4**	59.6		
PC-2	14.32	2.9212 ^d	27.7**	72.3		

+ = 0.07 > P(%) > 0.05, * = 0.05 > P(%) > 0.01, ** = P(%) < 0.01

^a The first character in the trait code designates the nursery environment, warm (W) and cool (C), the next 2 characters the trait, the first numeral the growing seasons, the second the place in any sequence of measurement; for example, WHT22 is the warm-bed total height, second season, second measurement. Traits are total height (HT), bud flush (BB), total diameter (DI), mean germinant rate of 50 seeds (MN), standard deviation of rate of germination (DRSD), seed weight of 200 seeds (SDWT), and cotyledon number (CO).

^b Total variance for height and diameter is among-location variance (σ_s^2) + among-family variance (σ_f^2) + plot variance (σ_p^2) + within-plot variance (σ_w^2). Total variance for seed trait is $\sigma_s^2 + \sigma_f^2 + \sigma_p^2$. Total variance for factor scores of principal component is $\sigma_s^2 + \sigma_f^2$.

^c Analysis based on all trees: 143 locations, 31 families within locations.

^d Analysis based on Cascade trees: 115 locations, 31 families within locations.

additive variance) plus microenvironmental variation among seedlings in rows. Cotyledon number, stem diameter, and mean rate of seed germination did not vary among locations, whereas bud burst did not vary among locations or among families within locations. On the other hand, seed weight, variability in rate of seed germination, and most height traits, varied both among and within locations. Table 3 provides a sample of analyses to illustrate results from different environments and years.

Table 4—Structural relations ($\times 100$) in the variability among seedlings^a

Trait ^b	(1) σ_s/\bar{x}	(2) σ_A/\bar{x}	(3) $\sigma_s^2/(\sigma_s^2 + 3\sigma_{f(s)}^2)$	(4) $2\sigma_{f(s)}^2/\sigma_w^2$	(5) σ_p/\bar{x}	(6) σ_w/\bar{x}	(7) h^2
WHT11	8.0	14.6	23.0	47.3	12.2	17.3	41.0
WHT31	14.1	20.5	32.1	47.8	12.3	24.3	48.0
WHT38	13.7	17.4	38.4	38.9	11.6	22.8	40.2
WHT41	14.1	18.1	37.5	40.0	12.0	23.4	41.0
WHT42	13.7	20.3	31.3	41.8	13.5	25.6	42.2
CHT21	9.3	10.7	43.0	31.7	9.4	15.5	31.2
CHT35	8.2	14.0	25.6	35.5	7.7	19.1	39.8
CHT36	12.0	20.5	25.5	43.9	13.3	25.3	44.0
WDI4	9.7	19.5	19.9	52.6	15.7	21.9	44.5
CDI3	5.5	14.5	12.7	39.1	4.9	19.0	46.5

^a Illustrated by coefficients of variation for locations ($100\sigma_s/\bar{x}$), additive genetic variation ($100\sigma_A/\bar{x}$), plot variation ($100\sigma_p/\bar{x}$), within-plot variation ($100\sigma_w/\bar{x}$), heritability (h^2) at the individual seedling level ($\sigma_A^2/(\sigma_A^2 + \sigma_p^2 + \sigma_w^2)$), where $\sigma_{f(s)}^2$ is the variance of families within locations and additive genetic variation is $3\sigma_{f(s)}^2$.

^b The first character in the code designates the nursery environment, the next 2 characters the trait, the first numeral the growing season, the second the place in any sequence of measurement; for example, WHT31 is the warm-bed total height, third season, first measurement. Traits are total height (HT), bud flush (BB), total diameter (DI), mean germination rate of 50 seeds (DRMN), standard deviation of rate of germination (DRSD), seed weight of 200 seeds (SDWT), and cotyledon number (CO).

As indicated by the high heritabilities of traits (table 4, col. 7), a large part of the variation among seedlings could be attributed to additive genetic effects. Although the component of variance for locations was generally larger than for families within locations (table 3), the coefficient of additive genetic variation (table 4, col. 2) was larger than the coefficient of genetic variation among locations (col. 1); location variation often made up less than one-third of total genetic variation (col. 3). Because additive variation contributed such a high proportion of the within-plot variance (col. 4), the coefficient of within-plot variation (col. 6) was only slightly larger than the coefficient of additive variation (col. 2).

On average, the estimated absolute values of genetic correlations among a sample of traits (table 5) were slightly higher for families (0.76) than for locations (0.68). This was noticeable particularly in correlations involving first-year height in the warmed nursery bed (WHT11). The exception occurred in DRSD (variation among seeds in rate of germination) where estimates of correlations for locations were much larger than estimates for families; except for the correlation of DRSD and seed weight (SDWT), coefficients for locations were large and negative, and for families, small and positive (table 5).

Large genetic correlations among a set of traits indicate control of the traits by similar gene complexes (pleiotropic effects or linkage disequilibrium), which can be indexed by creating one or more new variables, each correlated strongly with several of the original variables. To do this, the genetic correlation matrix for locations was subjected to a principal component analysis. For the analysis, several traits were deleted from the total matrix, usually because variation for these traits among locations was exceptionally small, which created very large errors in estimates of correlations.

Table 5—Genetic correlation coefficients and standard errors (In parentheses); above diagonal for locations, below diagonal for families in locations

	WHT11 ^a	WHT31	WHT38	WHT41	WHT42	CHT21	CHT35	CHT36	SDWT	DRSD
WHT11	1.00	0.44	0.45	0.38	0.25	0.65	0.02	−0.28	0.39	0.08
		(0.23)	(0.21)	(0.23)	(0.27)	(0.14)	(0.40)	(0.45)	(0.23)	(0.27)
WHT31	.82	1.00	1.01	1.02	1.02	.56	.66	.97	−.64	−.93
	(.10)		(.00)	(.00)	(.00)	(.17)	(.18)	(.14)	(.35)	(.43)
WHT38	.83	.97	1.00	1.01	1.01	.60	.66	.97	−.58	−.94
	(.14)	(.08)		(.00)	(.06)	(.15)	(.17)	(.14)	(.31)	(.41)
WHT41	.85	.97	.99	1.00	1.01	.58	.65	.95	−.61	−.97
	(.10)	(.09)	(.18)		(.05)	(.16)	(.17)	(.13)	(.32)	(.41)
WHT42	.74	.88	.89	.93	1.00	.58	.61	.95	−.70	−1.11
	(.11)	(.13)	(.19)	(.27)		(.16)	(.18)	(.11)	(.33)	(.45)
CHT21	1.30	.77	.74	.78	.68	1.00	.72	.37	−.57	−.19
	(—)	(.27)	(.23)	(.36)	(.47)		(.12)	(.18)	(.16)	(.27)
CHT35	1.29	1.09	1.14	1.19	1.14	1.18	1.00	.65	−.37	−.68
	(—)	(.23)	(.31)	(.40)	(.69)	(—)		(.16)	(.38)	(.41)
CHT36	1.11	.94	.92	1.06	1.08	1.02	1.07	1.00	−.94	−1.20
	(—)	(.20)	(.27)	(.35)	(.64)	(—)	(—)		(.45)	(.47)
SDWT	.99	.68	.67	.66	.49	.50	.70	.68	1.00	.86
	(.00)	(.18)	(.22)	(.26)	(.34)	(.06)	(.08)	(.10)		(.37)
DRSD	.06	.24	.27	.24	.21	.41	.05	.10	−.07	1.00
	(.24)	(.23)	(.25)	(.25)	(.26)	(.24)	(.25)	(.24)	(.31)	

^a The first character in the code designates the nursery environment, the next two characters the trait, the first numeral the growing season, the second the place in any sequence of measurement; for example, WHT22 is the warm-bed total height, second season, second measurement. Traits are total height (HT), bud flush (BB), total diameter (DI), mean germination rate of 50 seeds (DRMN), standard deviation of rate of germination (DRSD), seed weight of 200 seeds (SDWT), and cotyledon number (CO).

The first two principal components explained about 97 percent of the variation in all traits among locations. Loadings indicated that factor scores of the first principal component (PC-1) correlated strongly with height in the third and fourth growing season, regardless of environment (table 6). Larger scores in PC-1 were associated with greater heights and less variation in rates of germination among seeds in a family lot. Larger factor scores in the second principal component (PC-2) reflected mainly taller early heights and greater seed weight.

Factor scores calculated for each family were analyzed in two different groupings of families. In the first, the variance among all locations, including those not in the Cascade Range, accounted for 61 percent of the variance among all families for PC-1 and 40 percent for PC-2 (table 3). In the second analysis, variance among locations from the Cascades Range accounted for 49 percent of variance in all Cascades families for PC-1 and 28 percent for PC-2.

Table 6—The two main principal components (PC), their loadings with traits, the variance of their factor scores (eigenvalue), and their contribution in explaining variation among all traits (as a percentage)

Trait ^a	PC-1 ^b	PC-2 ^c
WHT11	0.306	0.885
WHT31	1.003	.060
WHT32	.996	.062
WHT33	.999	.075
WHT34	.998	.054
WHT35	1.004	.072
WHT36	1.008	.061
WHT37	.999	.064
WHT38	.998	.095
WHT41	1.003	.053
WHT42	1.025	-.046
CHT21	.561	.761
CHT35	.701	.076
CHT36	.098	-.427
SDWT	-.652	.764
DRSD	-.961	.402

^a The first character in the code designates the nursery environment, the next two characters the trait, the first numeral the growing season, the second the place in any sequence of measurement; for example, WHT22 is the warm-bed total height, second season, second measurement. Traits are: total height (HT), bud flush (BB), total diameter (DI), mean germination rate of 50 seeds (DRMN), standard deviation of rate of germination (DRSD), seed weight of 200 seeds (SDWT), and cotyledon number (CO).

^b Eigenvalue, 13.277; percentage of total variation 83.0.

^c Eigenvalue, 2.339; percentage of total variation 14.6.

For the analysis relating factor scores of parent trees to habitat indexes, an adjustment was made in elevation. Height of timberline in the Cascade Range decreases regularly from the California border north into Washington. Because white pine is more prevalent in upper slope habitats, elevations of the sample locations tended to follow the same trend. To simplify the regression analysis, the elevation of parent trees was adjusted to latitude by a relation (elevation in m = 5621.2 - 97.4 × latitude in degrees) that explained 28 percent of the variation in elevation of parent trees. Elevation values, as an index of environment, are made more commensurable over a range of latitude by this procedure. Phenological events, for example, are expected to differ by 4 days per degree of latitude or 122 m in elevation (Hopkins 1918). The procedure also increased the percentage of sums of squares explained in regression of factor scores by about two points for each principal component.

Table 7—Regression analyses of factor scores from principal components

Variable ^a	Principal component 1			Principal component 2		
	Partial coefficient	Significance P(b = 0)<...	Standardized coefficient	Partial coefficient	Significance P(b = 0)<...	Standardized coefficient
DL	0.3256	0.004	285.72	0.3400	0.043	232.78
D	-7.5280	.004	-145.27	-7.7743	.044	-117.06
DL2	-.3515E-02	.004	-140.95	-.3707E-02	.043	-115.97
L	7.3526	.013	9.41	-15.8591	.001	-15.84
L2	-.7747E-01	.018	-9.00	.1735	.001	15.72
E	-.1188	.002	-.24	-.5437E-02	.000	-.38
DLE				-.9270E-04	.040	-.19
CONST	-167.6811	.013		376.2725	.001	

Probability of lack of fit for PC-1 is 0.32; R² = 0.44.

Probability of lack of fit for PC-2 is 0.41; R² = 0.26.

^a D = distance east (+) and west (-) of the crest of the Cascade Range in kilometers, L = latitude in degrees, E = X/100 where X is elevation in meters adjusted for the average elevation of seed sources in the Cascade Range (see text), and CONST = constant.

Regression of factor scores on habitat indexes (latitude, distance from the crest, adjusted elevation) accounted for only part of the sums of squares in factor scores of families, 44 percent for PC-1 and 26 percent for PC-2 (table 7). The remaining unexplained variation apparently could be attributed to variation caused by sampling among trees at a location—lack of fit could not be shown for either regression equation (table 7). As suggested by the standardized regression coefficients (table 7), most of the accountable variation among parent-tree locations reflected a combined effect of latitude and distance west to east across the crest of the Cascades. Although elevation of parent trees differed considerably at any given latitude (fig. 1), adjusted elevation had an extremely small influence on differences in factor scores among locations.

Families with smallest height-growth potential and largest variation in rates of germination among seeds came from east of the Cascade crest in southern Oregon. Predictions from regression indicated factor scores of PC-1 were lowest in that region (fig. 3). At any given latitude and distance from the crest, growth potential was slightly poorer the lower the elevation (fig. 2a, b, c).

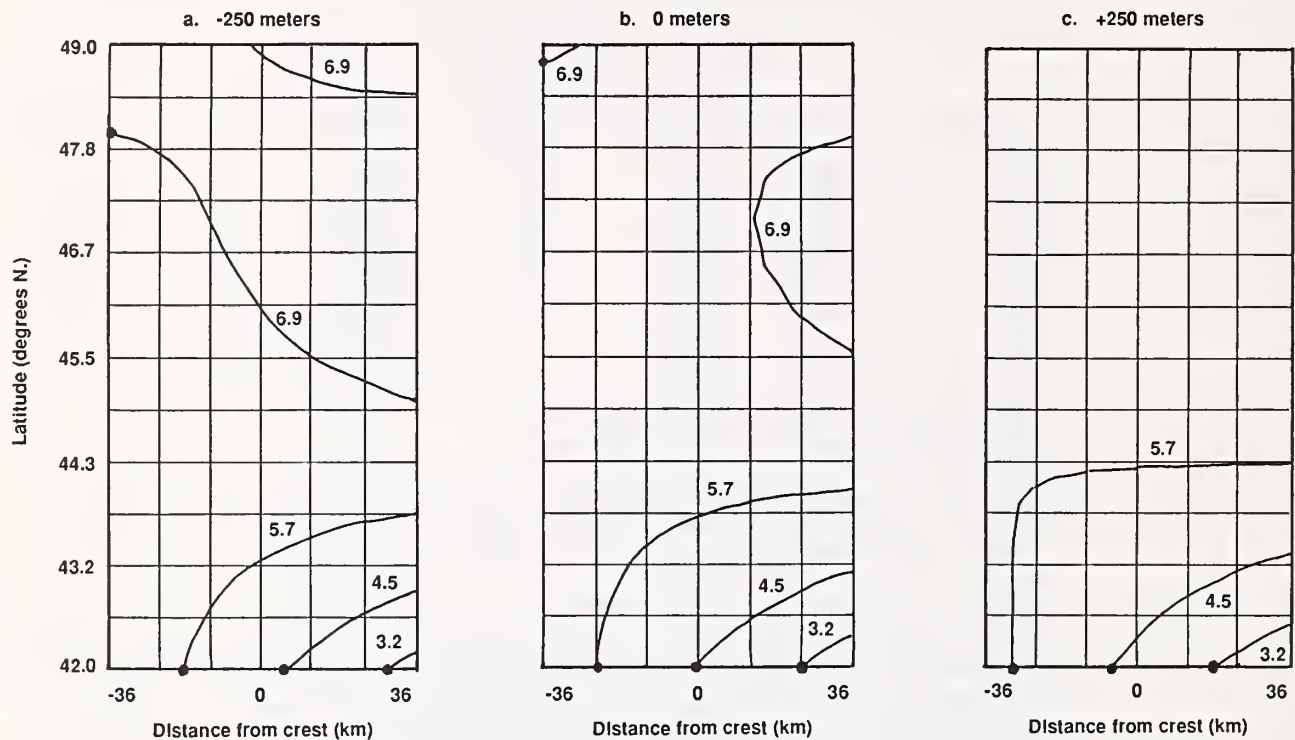


Figure 3—Predicted average genotypic values (factor scores of the first principal component) of white pine trees in the Cascade Range of western Washington and Oregon. Isolines are labeled with score values: (A) sites at 250 m below the average elevation of parent trees, (B) sites at the average elevation of parent trees, and (C) sites at 250 m above the average elevation of parent trees. The average elevation of trees decreases from south to north by the following relation: elevation in meters = $5621.2 - 97.4 \times \text{latitude in degrees}$.

Families with lowest seed weight and least growth in the first year came from high-elevation areas west of the crest of the Cascade Range and centered on the Columbia River. As indicated by factor scores for PC-2, seed weight and early growth increased north and south from this area to reach their largest values in southwestern Oregon (fig. 4a, b, c).

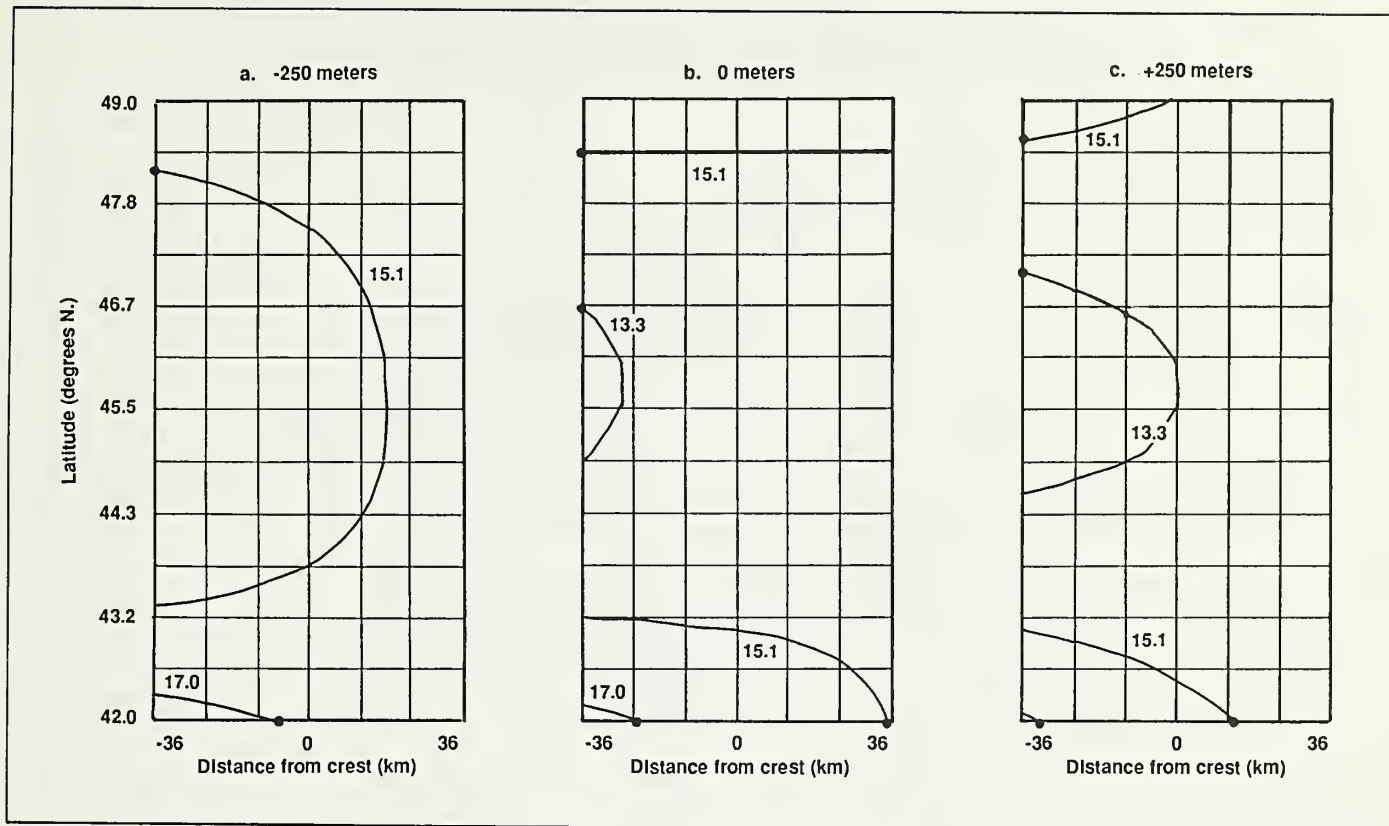


Figure 4—Predicted average genotypic values (factor scores of the second principal component) of white pine trees in the Cascade Range of Washington and Oregon. Isolines are labeled with score values: (A) sites at 250 m below the average elevation of parent trees, (B) sites at the average elevation of parent trees, and (C) sites at 250 m above the average elevation of parent trees. The average elevation of parent trees changes with latitude.

The relatively small amount of geographic variation (figs. 3 and 4) and the large amount of within-location variation (tables 3 and 4) made it possible to meet most zoning goals by creating five zones in the Cascades. Two of the zones fell wholly in Oregon, two wholly in Washington, and one fell in both States by extending across the Columbia River (fig. 5). The two zones in the Washington Cascades adjoined one another at the crest of the Cascades. Simulated transfers indicated that transfers within zones usually would create a risk index of less than 0.5 (table 8). Zones apply only to the areas sampled in the Cascade mountains (figs. 1 and 2).

Four provenances other than the Cascades provenance were also sampled. Differentiation of these provenances from the part of the Cascades provenance directly east or west (fig. 5) revealed significant variation (by multivariate analysis of factor scores) among the sampled provenances in southern Oregon (table 9). The hypothesis that Strawberry Mountain and northeastern Washington provenances are not differentiated from the Cascades provenance could not be disproved. But these tests, especially, lacked power in this experiment because very few trees were sampled in the non-Cascades provenances.

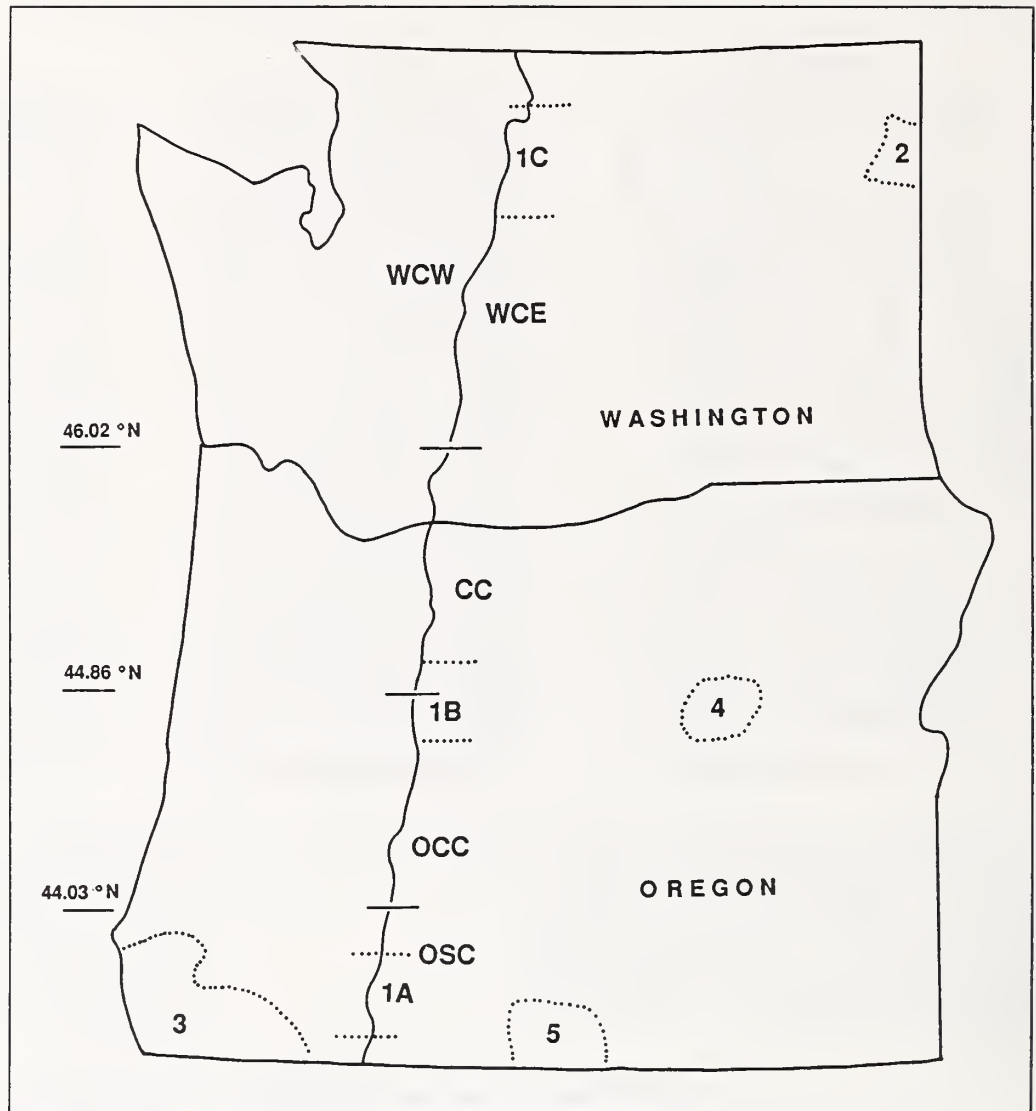


Figure 5—The latitudinal dimensions of provisional seed zones within the Cascade Range. Starting at the northern California border, the northern boundaries of zones are OSC—northern boundary of Crater Lake National Park (at 44.03 N. latitude); OCC—northern boundary of Mount Jefferson Wilderness (at 44.86 N. latitude); CC—a west-east line between Mount St. Helens and Mount Adams (at 46.02 N. latitude). WCW and WCE adjoin at the crest of the Cascade Range in Washington. Areas bordered by dashed lines include origins of families used to test differences (table 9) between Cascades and non-Cascades populations.

Table 8—Statistics of predicted risks in 200 simulated transfers between white pine sites within each of the 5 seed and breeding zones

Zone ^a	Transfer risk		Percentage of transfers with risks greater than indicated by the mismatch index (M) ^b	
	Average	Maximum	Percent	>Mi
1. WCW-Washington Cascades-west	0.22	0.54	2.0	0.48
2. WCE-Washington Cascades-east	.22	.62	2.5	.50
3. CC-Central Cascades	.19	.63	4.0	.52
4. OCC-Central Oregon Cascades	.23	.61	1.5	.48
5. OSC-Southern Oregon Cascades	.24	.60	3.5	.50

^a See figure 5 for locations of zones.

^b For example, the mismatch index (M) in the *i*th zone: if *i* = 5 = southern Oregon Cascades, then 3.5 percent of 200 simulated transfers in this zone had predicted risks greater than M = 0.50.

Table 9—Comparison of genotypic values of trees (factor scores) from Cascade provenances within latitudinal regions with values in provenances east or west of the Cascades

Regions and provenances ^a	Number of trees	Factor-score means		Wilks' test of probability of differences among provenances within regions		
		PC-1	PC-2	PC-1	PC-2	PC-1 and PC-2
Southern Oregon:				0	0.004	0.001
1A	13	5.00	15.25			
3	14	5.51	16.73			
5	7	3.14	13.72			
Northern Oregon:				.251	.776	.251
1B	8	6.57	14.37			
4	3	4.80	14.52			
Northern Washington:				.837	.340	.440
1C	9	6.67	14.50			
2	4	7.51	15.26			

^a 1A, 1B, 1C are Cascade Range provenances; others are provenances of non-Cascade origin. See figure 5 for location.

Discussion

The structure of genetic variation in the white pine of the Cascade Range was very similar to that found in white pine elsewhere (Rehfeldt 1979, Steinhoff 1979). Genetic variation among trees seems to reside mainly among individuals within populations, with only small amounts occurring among populations. Latitude and distance from the crest of the Cascades accounted for most of the population variation. As in other reports, little variation was associated with local elevation. Aspect and other indexes of local environment of parent trees were not measured, so microgeographic genetic variation could not be assessed. Evidence adding to previous reports of microgeographic variation, either supporting (Squillace and Bingham 1958) or refuting (Rehfeldt 1979) its occurrence, therefore could not be obtained.

The pattern of geographic variation in the Cascade Range also confirmed that reported previously (Rehfeldt and others 1984). Steepest gradients occurred south to north in the Cascades of southern Oregon, with additional gradients east to west in that area. Relatively little variation was found north of central Oregon. These differing levels of geographic variation coincided with apparent differences in environmental heterogeneity. The distribution of white pine in the Cascades rises from north to south at a rate (97 m per degree of latitude) nearly corresponding to Hopkins' (1918) bioclimatic "law" of equivalent phenologies (122 m per degree of latitude). Temperatures in white pine habitats therefore should be similar along the latitudinal range of white pine in the Cascades. On the other hand, precipitation sharply decreases southward to the California border, where it is one-third as much as in the northern Cascades (Franklin and Dyrness 1973). Along the upper slopes in the northern two-thirds of these mountains, white pine and noble fir (*Abies procera* Rehder) are seral species within the same forest zones. In these zones, both white pine (Rehfeldt and others 1984) and noble fir¹ show little genetic differentiation associated with latitude or elevation though, on the whole, white pine expresses less geographic variation than does noble fir. South of central Oregon, the genetic character of white pine changes abruptly (Rehfeldt and others 1984), as does the character of the *Abies procera*-*Abies magnifica shastensis* complex (see footnote 1). In the white pine of southern Oregon, geographic variation, which reflects strong precipitation gradients in the area, becomes a more prominent component of the total genetic variation among trees. In this same area, white pine becomes a more dominant member of the seral complex than it is elsewhere in the Cascades (Franklin and Dyrness 1973).

Because only a small proportion of the genetic variation in white pine occurs among populations, the suggested breeding zones in the Cascade Range are quite large. This does not imply, necessarily, that a seed lot transferred within a zone is adapted to all potential planting sites within the zone. White pine occurs naturally in scattered small stands and as individuals in the patchy distribution expected in a minor seral species. This patchiness precluded uniformly sampling parent trees for habitat or geography within the zone. Strictly speaking, therefore, zones have meaning only for areas presently occupied by white pine. Using white pine elsewhere within the zone carries with it a risk not accounted for by the model. The degree of risk depends on factors of the species' adaptive biology not yet clearly understood.

¹ Sorensen, Frank C.; Campbell, Robert K.; Franklin, Jerry F. Geographic variation in growth and phenology of seedlings of the *Abies procera*-*Abies magnifica* complex. Manuscript in preparation.

A species has two major ways of dealing with the environmental diversity among and within locations (Emlen 1975, Levin 1977); it can rely on somatic plasticity or it can generate many genotypes, thus creating genetic variation. Theoretically, a species leans heavily toward one or the other strategy (Thoday 1953). If the former strategy prevails, natural selection tends to make variation among individuals more and more phenetic; if the latter, more and more genetic (Emlen 1975).

Regardless of the major strategy for dealing with environmental heterogeneity, the species has the problem of balancing potentials for stability and flexibility within its genome. Thoday (1953) recognized that any unit of evolution must have both stability and flexibility. Stability is needed to track the common elements of the environment that occur from generation to generation, flexibility to meet the inevitable perturbations (Levin 1977).

These various alternative strategies for accommodating heterogeneity suggest at least three possible explanations for the genetic structure of white pine in the Cascade Range: (1) white pine may be exhibiting an unusual amount of somatic plasticity, (2) white pine may be occupying sites with environments that are not greatly different from site to site, and (3) white pine's genome may be emphasizing flexibility at the expense of stability.

Several things suggest that plasticity is not the primary means by which white pine survives diversity in the Cascades. In itself, the large amount of genetic variation within white pine populations is difficult to reconcile with a hypothesis of high plasticity within individuals; the combination is theoretically unlikely (Emlen 1975). The coefficients of additive genetic variation found in this experiment were at least as large as those found for similar traits in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Campbell and others 1986) and in Sitka spruce (*Picea sitchensis* (Bong.) Carr.),² and, moreover, were as large as those found in the *Abies procera*-*Abies magnifica shastensis* complex that mingles with white pine in high forests in the Cascade Range (see footnote 1).

At the individual seedling level, white pine apparently is no more somatically plastic than are other species displaying far more geographic variation. In this experiment, a genetic response rather than a plastic response to environment accounted for about 40 percent of the variation among individual seedlings. Heritabilities of this magnitude compare favorably with heritabilities in other Pacific Northwest species (Campbell and others 1986, see footnote 2) and are not expected in species with high plasticity.

Evolution nevertheless may have followed an unusual mode in white pine. Plasticity may have evolved to accommodate the components of environment that are stable from generation to generation and different among locations, leaving genetic variation to accommodate only the components that are spatially or temporally variable at a location. This does not seem likely, however, because somatic plasticity implies the presence of alleles with broad environmental tolerance (Rehfeldt and others 1984), and white pine has a rather restricted niche for shade tolerance, drought, (Franklin and Dyrness 1973), and cold (Bingham and others 1971, Daubenmire 1966).

² Campbell, Robert K.; Pawuk, William H.; Harris, Arland S. Microgeographic genetic variation of Sitka spruce in southeastern Alaska. Manuscript in preparation.

If white pine uses genetic variation rather than plasticity to withstand heterogeneity, as do other neighboring species, and if white pine displays large amounts of variability and moderate heritability, as do these other species, why does it not also generate geographic and microgeographic variation, as do these other species? One possibility is that the environments in the various habitats of white pine are so similar that genetic differentiation is not needed. Another is that the environments, although different, are highly variable among generations, and genetic differentiation consequently cannot be stabilized.

White pine can be found in several vegetation zones in the coastal and interior regions (Daubenmire and Daubenmire 1968, Franklin and Dyrness 1973), where it exists in company with Douglas-fir, western larch (*Larix occidentalis* Nutt.), western red cedar (*Thuja plicata* Donn ex D. Don), and other species, often across an elevational range of 1000 m. Within the regions, the species clearly occupies environments that are variable in moisture and cold stress. Its reaction to these environments is quite different in the two regions, however, as indicated by its importance in forest communities. The place of white pine in the *Tsuga heterophylla* zone provides an example: it is in this zone in northern Idaho that the well-known western white pine forests are best developed. Yet, in this zone in western Washington and Oregon, white pine is a very minor seral species, confined to uncommon habitats easily identified as having some features severely restricting growth or reproduction of the dominant species (Franklin and Dyrness 1973).

The distribution of white pine reflects its niche (its genetically mandated requirements for resources and its tolerance of conditions) and the occurrence of habitat satisfying this niche. Its limited representation in coastal forests may indicate a circumscribed niche or lack of an appropriate habitat. According to Daubenmire (1966), its requirements and tolerances in the interior region occupy a rather narrow central position on the warm-dry to cool-wet continuum of environments. The coastal region should supply habitats in profusion to satisfy this niche. The *Tsuga heterophylla* zone, for example, in which white pine thrives in northern Idaho, occupies about half of the area west of the Cascade crest. Yet, in the coastal region, white pine prevails commonly in the more extreme environments in localities where it is found. It seems more likely, therefore, that white pine's realized niche (its requirements and tolerances under competition) differs in the two regions. The niche is much narrower in the coastal region than in the inland region. In the coastal region, the seral tree species associated with white pine differ from zone to zone and apparently determine the uncommon habitats it will be restricted to. Though some of these species are found in both regions, coastal varieties of seral species such as Douglas-fir are usually faster growing than interior varieties (Emmingham 1977, Haddock and others 1967). In contrast, interior provenances of white pine appear to grow as fast as coastal provenances (Steinhoff 1981), or perhaps even faster (Bower 1987). This may account for white pine's greater importance in interior vegetation zones than in coastal zones.

Western white pine can apparently occupy habitats of considerable environmental diversity. It seemingly accomplishes this with a small amount of genetic variation among provenances. That white pine has an uncommon capability for handling diversity cannot be inferred, however, from either its distribution or its apparent genetic structure. One can infer that a population of white pine can tolerate conditions and thrive over a certain range of environments on the warm-dry to cold-wet continuum, for example. But whether this range is greater than can be occupied by a comparable population of any wide-ranging, genetically variable seral species is not known. A comparison would be difficult; each species, or population within a species, may be adapted to occupy somewhat different possibilities along one or more environmental continua.

The environment associated with geography must be both diverse among locations and consistent among generations to generate geographic variation by natural selection; furthermore, a stable genomic reaction developed as an adaptation to a consistent environment must confer enough reproductive advantage to offset a loss in genomic flexibility (Bradshaw 1965). White pine is a minor seral species in most of its range. In this part, it apparently survives in habitat nooks, sheltered by chance or circumstance from competition with species better able to use the local resources or to tolerate the local conditions. As indicated by its minor seral position, it needs very special conditions to give it a telling competitive advantage during regeneration. These conditions undoubtedly fluctuate from generation to generation, depending on fire, timing of periodic cone crops, and other factors affecting the reproductive success of competitors. In some generations, only a few white pine trees may survive at some locations. With conditions and population size so dependent on chance, the environments affecting natural selection in white pine are probably inconsistent from generation to generation, and stability advantages gained in one generation may be lost by genetic drift in the next. Under these circumstances, the benefits of genomic flexibility may far outweigh the benefits of stability.

Three hypotheses can be invoked to explain the genetic structure of white pine in the Cascade Range: (1) the species is somatically plastic, (2) the habitat nooks the species is found in are environmentally homogeneous even though sometimes separated by hundreds of kilometers, and (3) the species emphasizes genomic flexibility at the expense of genomic stability. As yet, there seems to be no clear way to choose among the three hypotheses, if in fact, any one of them is correct.

In what respect do the hypotheses help guide decisions in seed transfer and in tree breeding? All suggest that seed zones can be quite large without greatly influencing adaptation. Whether transfers within zones can be made safely to areas presently lacking white pine, however, depends on the special conditions permitting white pine to survive within the zone. If white pine is limited to its present distribution mainly by competition, transfers throughout the zone should be safe, given appropriate silviculture. If white pine is also limited by access to, or tolerance of, special factors of the environment, the acceptable range of these factors must be identified; transfers would then be restricted to sites within this range. Because white pine is a minor or major seral species in many habitat types in northern Idaho (Rehfeldt 1979), and in

Washington and Oregon (Franklin and Dyrness 1973), it seems likely that competition is the major limiting factor. The safest course still would be to limit planting to sites recently occupied by white pine until long-term tests have established other possibilities.

According to the first and third of the hypotheses above, white pine has sacrificed adaptations to local conditions for the advantages of somatic or genomic flexibility. We might therefore expect it to be less well adapted to common conditions in a zone than are other more dominant seral species in that zone. Planting at higher than usual densities is one way to compensate for poor average adaptation to site (Campbell 1975, Campbell and Sugano 1987).

English Equivalents

When given:	Multiply by:	To find:
Meters (m)	3.282	Feet
Centimeters (cm)	0.39	Inches
Kilometers (km)	0.621	Miles
Hectares (ha)	2.471	Acres
Celsius (°C)	1.8 (and add 32)	Fahrenheit (°F)

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Provisional seed zones and breeding zones were developed for white pine (*Pinus monticola* Dougl. ex D. Don) in the Cascade Range of western Washington and Oregon. Recommendations were based on genetic variation patterns obtained by evaluating genotypes of trees from 115 locations. Genotypes controlling growth vigor and growth rhythm were assessed in common gardens. Five zones, delimited mainly by latitude, were recommended: two in Washington, two in Oregon, and one in both States adjoining the Columbia River.

Keywords: Genetic variation, geographic variation, adaptation (plant), seed-transfer, *Pinus monticola*.

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